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KIYOHIMEA USAGI, A NEW SPECIES OF LOBATE CTENOPHORE FROM THE MONTEREY SUBMARINE CANYON

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ABSTRACT

Kiyohimea usagi is the second species to be described in the monogeneric family Kiyohimeidae. *Kiyohimeidea aurita* possesses tentacular canals but no tentacular apparatus while *K. usagi* has both tentacular canals and tentacular apparatus. Observations and collections of *K. usagi* were made in Monterey Bay with a remotely operated vehicle between 200 m and 310 m in the Monterey Submarine Canyon. This paper describes *K. usagi*, distinguishes it from its congener, and presents in situ behavioral observations.

The difficulties inherent in working with ctenophores have been well documented (Harbison et al., 1978; Matsumoto, 1990b). The Phylum Ctenophora has representatives in virtually every ocean and has species that have been observed to inhabit the oceanic water column down to depths of at least 4,000 m (O'Sullivan, 1986). Historically, work on ctenophores has focused primarily on the neritic and shallow-water species because undamaged specimens of oceanic (epipelagic to abyssal) species were too difficult to collect with standard plankton sampling techniques. The more recent application of SCUBA to marine science, coupled with the techniques of blue-water diving have enabled researchers to examine the upper 35 m of the oceanic water column with greatly improved resolution (Hamner, 1975; Heine, 1986; Harbison et al., 1978). As a result of these and similar studies, our knowledge of the Phylum Ctenophora has been greatly expanded in the last two decades. The advent of research submersibles and the further exploration of even deeper waters has revealed an abundance of new ctenophore taxa, from the species to the ordinal level (Madin and Harbison, 1978a, 1978b; Matsumoto, 1990a, 1990b).

The family Kiyohimeidae was erected in 1940 to accommodate the new genus and species *Kiyohimea aurita* Komai and Tokioka. *Kiyohimea aurita* was described from the waters around the Seto Marine Biological Laboratory (East China Sea 33°N, 129°48'E) and has since been observed in the North Atlantic Ocean as well (Harbison, 1985a; pers. comm.). Herein we describe a new species, *Kiyohimea usagi*, in this monogeneric family. The specimens were first observed (1985) in Monterey Bay from the manned submersible DEEP ROVER, with subsequent (1989–1991) detailed observations and collections made with an unmanned vehicle.

METHODS

Extensive in situ observations and collections of *Kiyohimea usagi* were made with a remotely operated vehicle (ROV) working in the Monterey Submarine Canyon, around a principal dive site located at 36°42'N, 122°02'W (Fig. 1). The ROV, operated by the Monterey Bay Aquarium Research Institute, is an ISE Hysub 40, rated to 1,850 m (Barber, 1989; Etchemendy and Davis, 1991). The operational depth of the submersible was limited to the upper 600 m of the water column during the course of this study.

The ROV utilizes a broadcast quality color video camera (Sony DXC 3000) equipped with a surface-controlled zoom lens that provides wide-angle, telephoto, and macro-imaging capabilities. The video signal is routed to the surface support ship (R/V POINT LOBOS) through optical fibers at the core of the ROV's tether cable. At the surface, the video signal is recorded on high resolution videotape (RGB in Betacam format). The ROV also carries a CTD unit with real-time readout at the surface, and paired lasers which provide a spatial size reference on the recorded video image.

Verbal descriptions by the scientist and vehicle pilot are simultaneously recorded onto the audio track of the video tape. These data are subsequently transcribed into the MBARI database (ALLBASE)

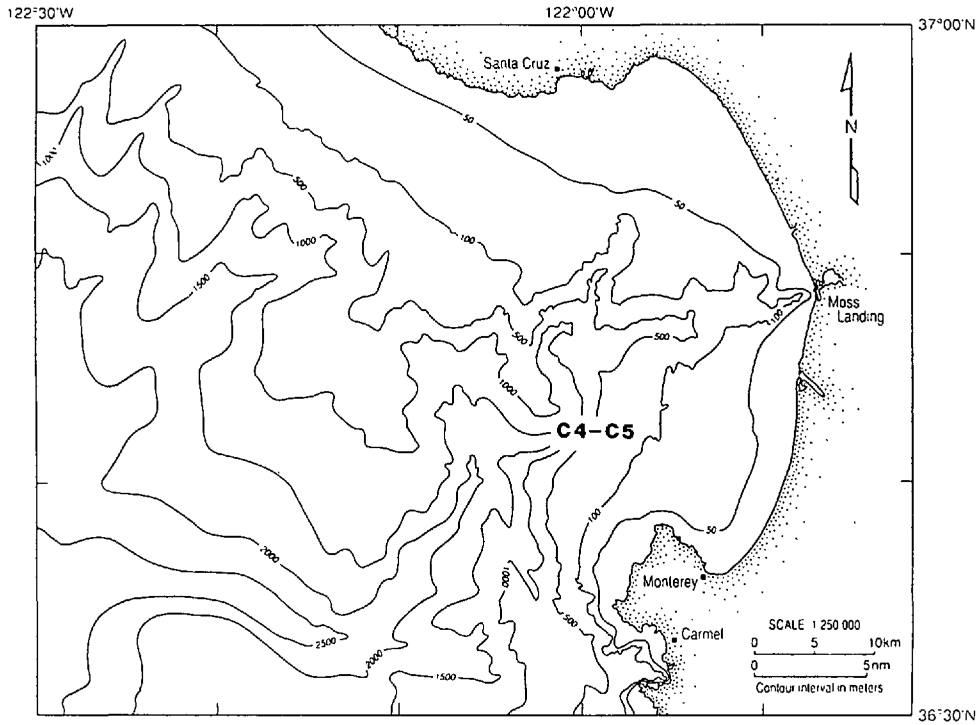


Figure 1. Remote vehicle operations were primarily at the dive site marked C4–C5 in the Monterey Canyon (36°42'N, 122°02'W).

and are timecode-linked to video frames, instrument readouts, and navigation data for both the ship and the ROV. Vehicle control functions are such that in situ observations of *K. usagi* lasting up 62 min were made without disturbing the individual. In situ observations of fragile, lobate ctenophores provide detailed information on their structure. Often, this morphological information is far superior to that which can be inferred from preserved material.

Specimens were collected using a 7.5-liter cylindrical sampler, developed by the Harbor Branch Oceanographic Institution for the gentle capture of delicate material in midwater. The pilot positions the ROV so that the sampler encloses the specimen, and then the top and bottom doors are hydraulically closed. Captured specimens were returned to the laboratory ashore for microscopic examination and eventual preservation in 4% buffered glutaraldehyde.

Order LOBATA Agassiz, 1860

Diagnosis.—Body compressed in tentacular plane forming a pair of large oral feeding lobes. Tentacles usually reduced in adults with no sheaths present. There are usually four ciliated processes (auricles) between the oral lobes.

Family Kiyohimeidae Komai and Tokioka, 1940

Diagnosis.—This is, as yet, a monogeneric family. Description is as for the genus. The family Kiyohimeidae was first described in 1940 (Komai and Tokioka) from a single "perfect specimen" and an unknown number of less than perfect specimens. At that time, the diagnostic characters for the erection of the new family, genus, and species included the presence of aboral processes without tentacles.

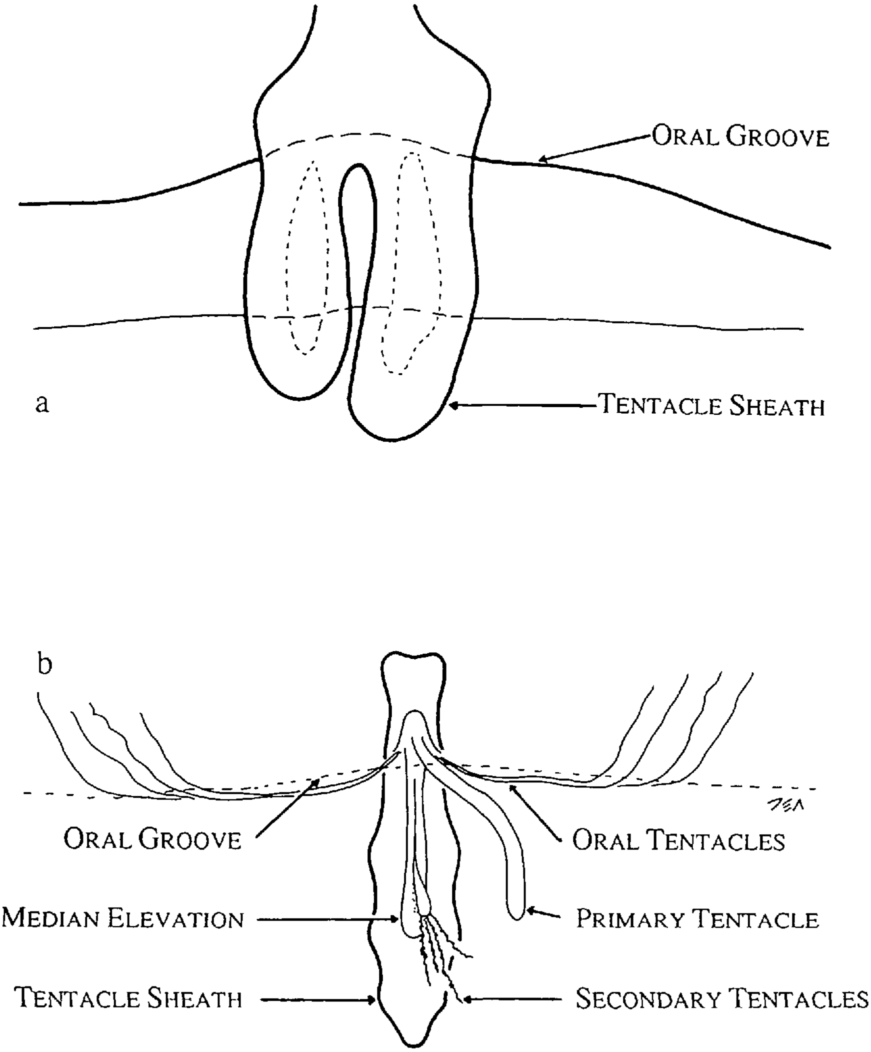


Figure 2. The tentacular apparatus of (a) *Kiyohimea aurita* (slightly modified from Komai and Tokioka, 1940) and of (b) *K. usagi* (from laboratory and in situ observations).

Genus *Kiyohimea* Komai and Tokioka, 1940

Diagnosis.—*Kiyohimea* is a large transparent lobate ctenophore with a V-shaped body that is greatly compressed in the tentacular plane. There are two aboral processes ranging in size from $\sim 1/10$ body length to $1/3$ body length. The substomadaeal ctene rows and substomadaeal meridional canals extend onto these processes. The ctene plates do not overlap and there is no pigmentation.

Kiyohimea aurita Komai and Tokioka, 1940

Diagnosis.—The only previously described species in this genus is *Kiyohimea aurita*. Komai and Tokioka (1940) remark on the absence of any tentacular apparatus (Fig. 3 in Komai and Tokioka; Fig. 2a here) as a characteristic of the genus. We consider this to be a characteristic of the species described in their

Table 1. Observations of *Kiyohimea usagi* have been made with a remote vehicle during cruises in the Monterey Submarine Canyon. Dates are given in both standard format and in Julian Days (JD). Time and duration of observations are in Greenwich Mean Time (GMT) and depths (in meters) and temperature (in °C) are listed whenever the data was available

Date (JD)	Time (GMT)	Depth	Temp
April 26, 1989 (116)	203355–213030	291	NA
May 2, 1989 (122)	161223–171540	240	NA
June 27, 1989 (178)	163049–165241	310	NA
Sept. 1, 1989 (244)	193717	287	7.6
Oct. 6, 1989 (279)	153924–154604	240	8.8
Nov. 15, 1989 (319)	215835–220331	260	8.2
Nov. 21, 1989 (325)	210942	268	8.1
Dec. 5, 1989 (339)	193032	304	7.5
Jan. 25, 1990 (025)	221208-221357	300	NA
Feb. 6, 1990 (037)	175144	295	NA
Feb. 20, 1990 (051)	194444-194556	305	8
May 8, 1990 (128)	172649–173119	200	NA
May 22, 1990 (142)	174553	249	7.6
May 29, 1990 (149)	193049	292	NA
July 2, 1990 (183)	190306	263	7.6
	195654	208	7.9
July 3, 1990 (184)	181148	351	NA
	~215003	299	NA
July 10, 1990 (191)	194912	225	8.6
Aug. 1, 1990 (213)	~191859	NA	NA
Oct. 2, 1990 (275)	204934–205111	340	NA
Dec. 11, 1990 (303)	191730	305	6.5
Dec. 20, 1990 (354)	~180004	201	8.6
Jan. 2, 1991 (002)	~224530	243	NA
Jan. 22, 1991 (022)	~232000	248	NA

paper—*K. aurita*. The specimens of *K. aurita* described in 1940 reached a body length of 8 cm and were extremely fragile.

Kiyohimea usagi new species
Figures 2–5

Type Material.—Twenty-five specimens have been examined with the MBARI ROV and two undamaged specimens have been collected (36°42′N, 122°02′W). *Kiyohimea usagi* has been observed on 23 of the 85 midwater dives that the ROV has made to date, and does not appear to exhibit any seasonality in its abundance (Table 1). Two specimens have been collected, with an average body length of 31.5 cm ± 1.5 (N = 2) and an average width of 4.0 cm ± 0.5 (N = 2) in the tentacular plane, and of 21.0 cm ± 4 (N = 2) in the stomodaeal plane. The holotype specimen has been placed into the collection of the California Academy of Sciences (CASIZ #075590).

Type Locality.—Monterey Submarine Canyon off the west coast of North America. The holotype was collected at 305 m at 36°42′N, 122°02′W on 11 December 1990.

Description.—The following description is based on video observations of 25 specimens and on laboratory observations of the two collected specimens.

GENERAL. The general body plan of *Kiyohimea usagi* is V-shaped with a distinct compression in the tentacular plane (Fig. 3). The entire ctenophore is colorless, the presence of tentacles (which may or may not be extended) is diagnostic of the species. The oral lobes originate at the level of the mouth and are at most ~½ body length. *Kiyohimea usagi* has been found in the water column from 200 m to 310 m and does not appear to move very rapidly or for any great distances. The terminology used in this paper is primarily that of Harbison and Madin (1982) and Harbison (1985b).

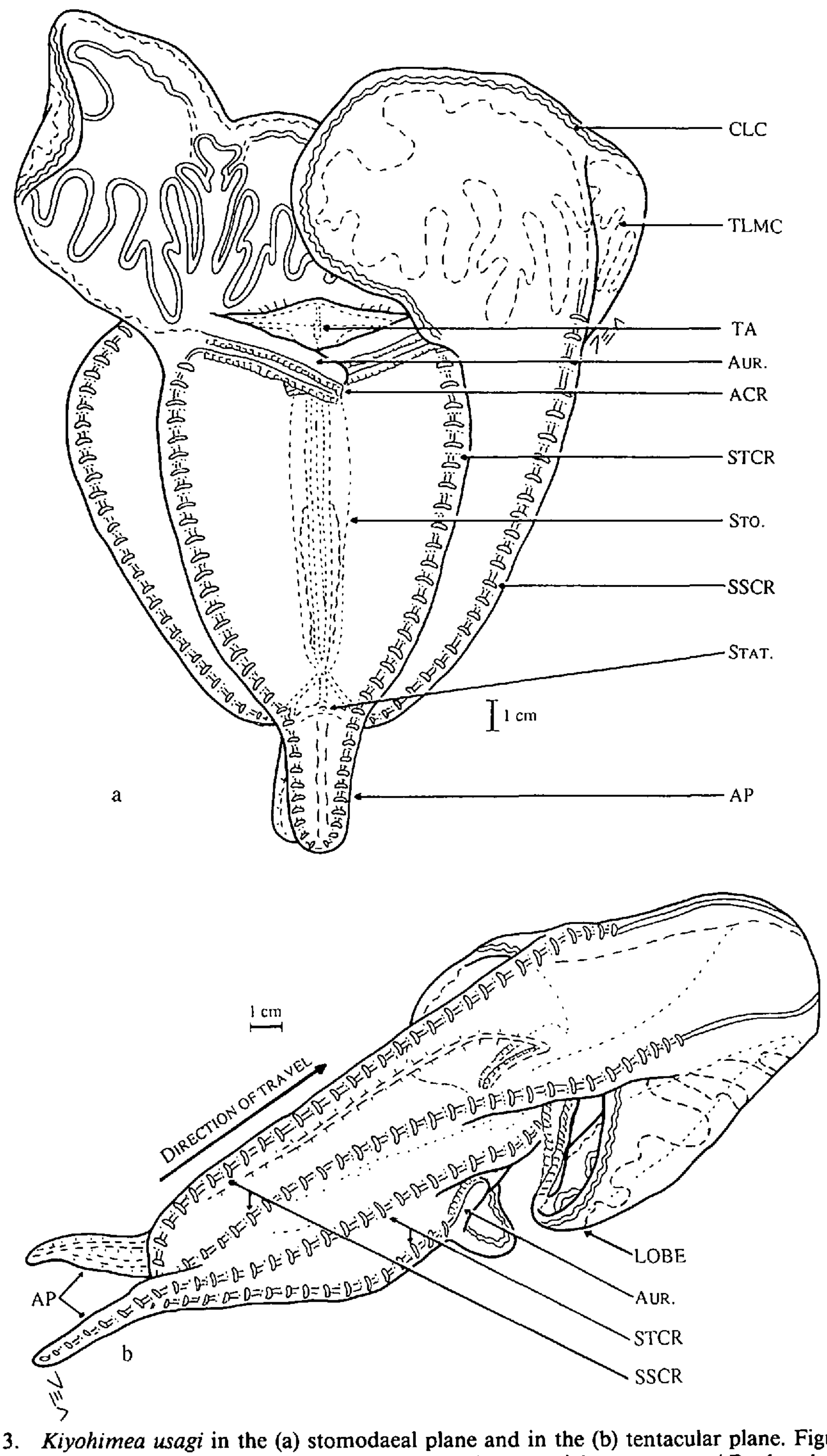


Figure 3. *Kiyohimea usagi* in the (a) stomodaeal plane and in the (b) tentacular plane. Figures are sketched from in situ video sequences. Abbreviations: ACR, auricle ctene row; AP, aboral process; Aur., auricle; CLC, circumlobal canal; Stat., statocyst; Sto., stomodaeum; SSCR, substomodaeal ctene row; STCR, subtentacular ctene row; TA, tentacular apparatus; TLMC, translobal meridional canal.

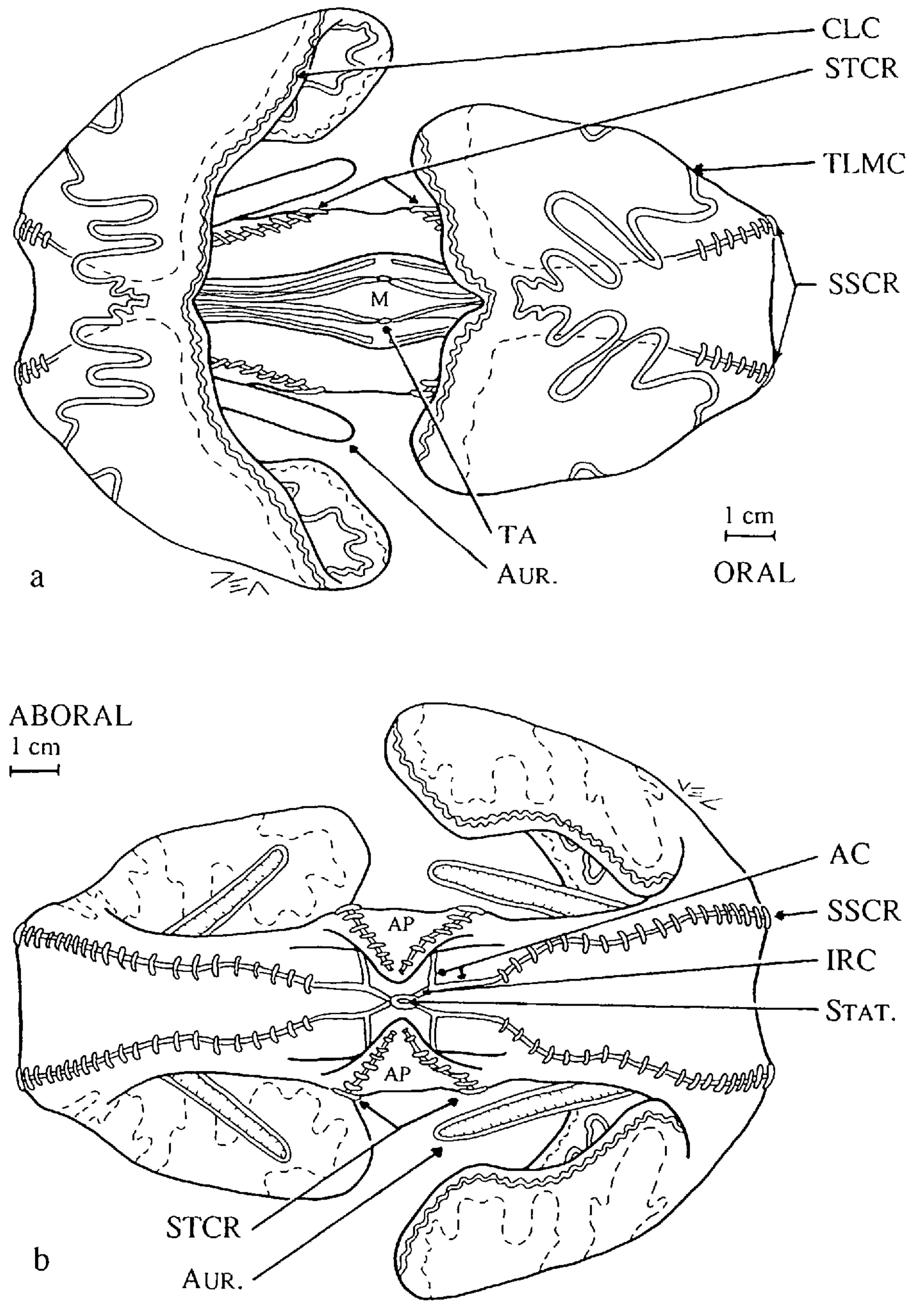
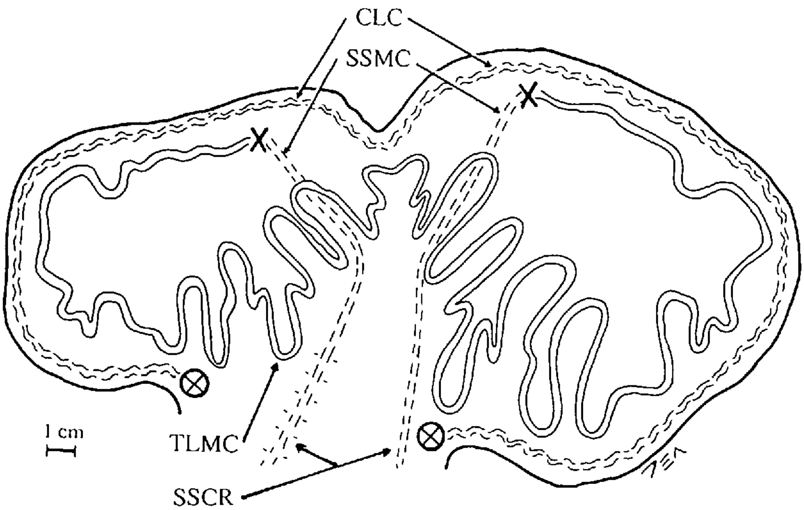


Figure 4. *Kiyohimea usagi* in an (a) oral view and in an (b) aboral view. Figures are sketched from in situ video sequences. Abbreviations: AC, adradial canal; AP, aboral process; Aur., auricle; CLC, circumlobal canal; IRC, interradial canal; M, mouth; Stat., statocyst; Sto., stomodaeum; SSCR, sub-stomodaeal ctene row; STCR, subtentacular ctene row; TA, tentacular apparatus; TLMC, translobal meridional canal.



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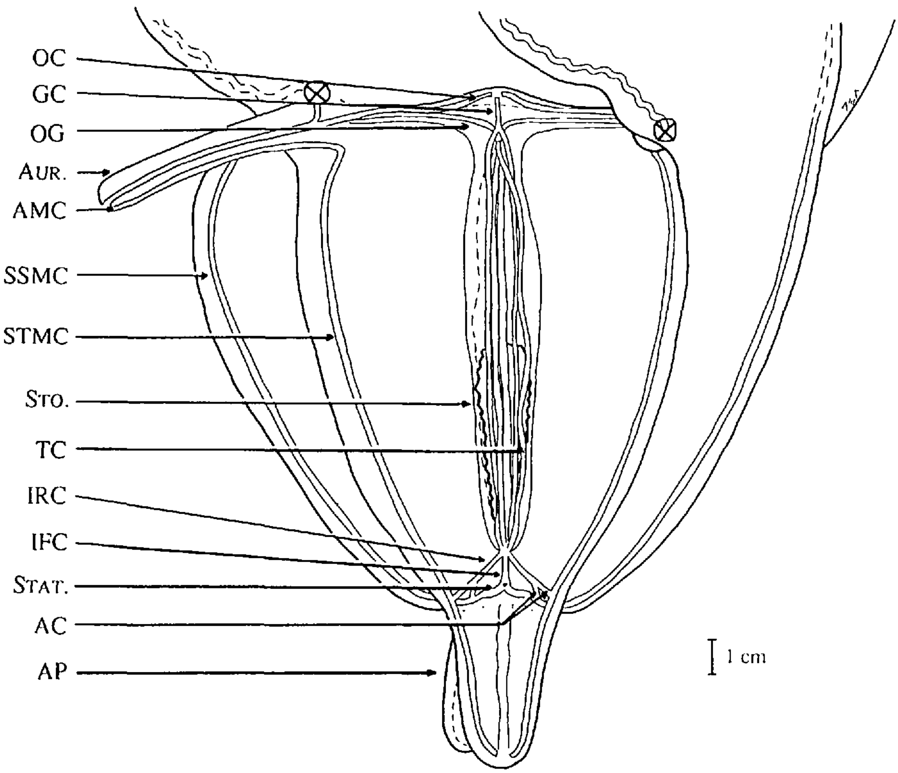

b

Figure 5. *Kiyohimea usagi.* (a) The lobe gastrovascular system of *K. usagi.* (b) The body gastrovascular system of *K. usagi.* Figure 3a and Figure 5b can be superimposed to obtain the complete morphology of *K. usagi.* Abbreviations: AC, adradial canal; AMC, auricular meridional canal; AP, aboral process; Aur., auricle; CLC, circumlobal canal; GC, gastric canal; Inf. C., infundibular canal; IRC, interradial canal; OC, oral canal; OG, oral groove; SSCR, substomodaeal ctene row; SSMC, substomodaeal meridional canal; Stat., statocyst; STMC, subtentacular meridional canal; Sto., stomodaeum; TC, tentacular canal; TLMC, translobal meridional canal; ×, spot where the SSMC passes into the lobe and becomes the TLMC; ⊗, spot where the circumlobal canal passes through the lobe and becomes the AMC.

TENTACLES. *Kiyohimea usagi* has tentacular canals and a tentacle bulb on each side of the mouth, in between the auricles. Each bulb has a large simple tentacle and numerous smaller tentacles. There are three types of tentacles (Fig. 2b). The primary tentacle is simple and stout and can reach up to at least the length of the body. At the base of this tentacle are a number of thinner tentacles (oral tentacles) that can extend along the oral groove. The median elevation of the tentacular apparatus extends orally and has four very short tentacles (labeled secondary tentacles in Fig. 2b) that originate from the oral end of the elevation.

AURICLES. There are typically four slender auricles that vary in length up to ¼ of the body length. Each auricle possesses a row of ctene plates, which beat with an antiplectic metachrony. The auricles of *Kiyohimea usagi* are usually extended at a slight angle away from the main body (Fig. 4) and do not move much from that position. The auricular ctene plates are almost constantly in motion.

LOBES. The oral lobes are typical of all other described species in the order Lobata. *Kiyohimea usagi* has lobes that originate from the level of the mouth and extend in front of the mouth up to ⅓ of the body length (Figs. 3, 5a). The lobes are often asymmetric with one lobe being markedly smaller than the other. The lobes and the mucus on their inner surfaces appear to be the primary food capture areas. Prey (e.g., euphausiids) were often observed to adhere to the mucus on the lobe. The lobes are extremely pliable, yet are tough enough to resist the forces exerted by euphausiid escape behavior. The mucus lining the inner lobe surface is often visible as strands that appear to be highly elastic; euphausiids stuck to the mucus strands have been observed to swim rapidly without being able to break the strand or the attachment.

CTENE ROWS AND CANALS. All ctenophores possess eight ctene rows at some time during their lives. A ctene row is composed of ctene plates which consist of linked macrocilia. The ctene rows beat with an antiplectic metachrony (where the effective or power stroke and the apparent stroke are in opposite directions). The position of the ctene rows, relative to the stomodaeal plane and to the tentacular plane (Fig. 3), determine the name of the ctene rows (i.e., SSCR: substomodaeal ctene row, STCR: subtentacular ctene row). The auricles also possess ctene rows (ACR: auricular ctene row).

Meridional canals lie under the ctene rows and are named relative to the associated row (i.e., SSMC: substomodaeal meridional canal, STMC: subtentacular meridional canal). These meridional canals link up with other canals to form the ctenophore gastrovascular system (Fig. 5). Examination of the SSCR reveals that it ends on the outer surface of the lobe. In contrast the substomadaeal meridional canals (SSMC) continue out onto the lobe for a short distance, before passing through the lobe to its inner surface (marked with an X in Fig. 5a), to join with the translobal meridional canal (TLMC). The TLMC undergoes a complex series of twists and turns before passing back up through the lobe, to link up with the SSMC from the adjacent SSCR. This pattern of winding is characteristic of the species and is similar for both lobes. There can be slight variation between individual animals or if a lobe is damaged. There is a circumlobal canal (CLC) that is continuous around the outer edge of the lobe under the external surface. The CLC joins the auricular meridional canal (AMC) on the underside of the lobe to the oral canal (OC). The point of transition for the CLC as it passes through the lobe is marked with an ⊗ in Figure 5a.

The subtentacular meridional canal (STMC) continues, in an oral direction, beyond the end of the STCR, becoming the auricular meridional canal (AMC) as it extends underneath the auricular ctene row (ACR). The auricular meridional

canal continues on and splits to form the circumlobal canal (CLC), the oral canal (OC), and the oral groove (OG). The OG stretches across the oral surface and both the primary and the oral tentacles are often located inside this groove. The OC follows the curvature of the oral region and dead ends near the midpoint (which is the highest point) of the oral region. The gastric or paragastric canals (GC) merge as they near the oral region and also dead end near the midpoint of the oral region. The GC leave the stomodaeum aborally and enter the infundibulum becoming the infundibular canal (Inf. C). Each of the eight ctene row meridional canals is directly or indirectly connected to this infundibular canal. The SSMC's continue aborally beyond the aboral ending of the SSCR and adradial canals branch off from the SSMC at the level of the statocyst. Adradial canals of adjacent SSMC and STMC fuse to form an interradial canal (IRC), which then fuses with the Inf. C at the base of the stomodaeum. Aborally, the STCR and the STMC continue out onto the aboral process where they dead end. There is an additional structure within the aboral process that resembles a canal and extends from near the aboral end of the process to just below the statocyst. An adradial canal intersects the STMC at the level of the statocyst. The tentacular canal (TC) originates at the base of the stomodaeum (where the four interradial canals and the Inf. C emerge) and gradually rises through the body to just under the surface. The TC continues orally to the tentacular apparatus.

Etymology.—The genus name, *Kiyohimea,* refers to Kiyohimé, the heroine of a Japanese legend. The species name, *usagi,* is a noun in apposition and is Japanese for rabbit and refers both to the legend and to the aboral processes which generated the informal name of "rabbit-eared ctenophore" for this species.

Behavior.—*Kiyohimea usagi* does not exhibit any of the rapid locomotory responses observed for other lobate ctenophores (Madin and Harbison, 1978a; Matsumoto, 1990b). There is very little movement of the ctenophore through the water. *Kiyohimea usagi* tends to drift with the water mass. The main ctene rows beat occasionally but the only obvious activity is the movement of the auricles and the auricular ctene rows (ACR). Even this activity is limited, and *K. usagi* appears to be a passive ambush predator, waiting for prey to contact the lobes where mucus effectively entangles the prey. Euphausiids entangled in mucus threads have been observed to swim for short distances away from the ctenophore, but the euphausiids do not seem to be able to break away.

Comparisons.—A possibly related genus is *Deiopea* which possesses smaller aboral processes and a more rounded body shape. It has been suggested that *Deiopea* may be a juvenile form of *Kiyohimea* (Harbison, pers. comm.). *Deiopea* has a similar oral canal system (where both the oral canals and the gastric canals end blindly), but has a different subtentacular meridional canal structure (STMC). In *Deiopea,* the STMC diverges from the STCR around the level of the statocyst while in *Kiyohimea,* the STMC continues under the STCR out into the aboral process. Haddock (pers. comm.) has observed the growth of the STCR of *Deiopea* and notes that the STMC does not extend with the growth of the ctene rows. The windings of the TLMC are much more simple in *Deiopea* which also has a more oval-shaped body than *Kiyohimea.* The number and placement of the ctene plates also separates these two genera as *Deiopea* has 8–30 widely spread ctene plates per ctene row, while *Kiyohimea* has more ctene plates per row that are more closely spaced. It is possible that *Kiyohimea* is an adult or later stage of *Deiopea,* but until further studies are made, this new and unusual ctenophore clearly belongs in the monogeneric family Kiyohimeidae.

Discussion

Based on the current literature and on our examination of both *Deiopea* and *Kiyohimea,* it is not clear that the two genera represent different life stages of one genus. There is a great deal of variation with regard to size of the aboral processes, lobes, and auricles. We postulate that this variability is due to regeneration of damaged areas. It is clear that *Kiyohimea aurita* and the species (*K. usagi*) observed in the Monterey submarine canyon are different. *Kiyohimea usagi* can reach up to 28 cm in body length and are relatively robust. There is a tentacular apparatus and three distinct types of tentacles in the area where *K. aurita* has none. The likelihood that the tentacular apparatus was missing from all of the specimens obtained by Komai and Tokiaka (1940) seems low. The presence of the tentacular apparatus and multiple tentacles, the often long aboral process, the complex windings of the TLMC in the lobes, and the blind canals in the oral region, clearly distinguish *Kiyohimea usagi* from its congener *K. aurita* in the monogeneric family Kiyohimeidae.

It is possible that future work will reveal the two genera (*Kiyohimea* and *Deiopea*) to be synonymous, but based on the present status of their taxonomy, we propose that *Kiyohimea usagi* be recognized as a new species in the lobate family Kiyohimeidae.

Acknowledgments

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